V. *On Variation in the Colour of Cocoons of* Eriogaster lanestris *and* Saturnia carpini. By William Bateson, M.A., Fellow of St. John's College, Cambridge. Communicated by Dr. David Sharp, M.A., F.R.S.

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It is well known that the cocoons of certain moths are sometimes dark brown and sometimes of various lighter shades of colour, being occasionally quite white. This variation is well known in the case of the Small Egger (*Eriogaster lanestris*), and the Emperor Moth (*Saturnia carpini*).

It has been suggested by Poulton* and others that these colours are of value as a means of concealment from enemies, and it has been stated by them that the variation in colour of these cocoons accords with that of the substances to which the cocoons are attached. In the place referred to, Poulton says:—"I found that caterpillars of this species (*S. carpini*) spun very dark brown cocoons in a black calico bag, while white cocoons were spun in white surroundings in a strong light. In this case it seems almost impossible for the surrounding colours to influence directly the colour of the cocoon. It is necessary to assume the existence of a complex nervous circle as a medium through which the stimulus of colour can make itself felt. . . . . The Rev. W. J. H. Newman showed that the cocoons of *E. lanestris* are creamy white when spun on white paper, dark brown when constructed among leaves. . . . . The fact that light reflected from green leaves is here the stimulus for the production of a dark colour is readily intelligible when we remember that the moth does not emerge till the following February at the earliest, while the insect often remains in the pupal state for one or two years longer. The leaves in contact with the cocoon soon die

* E. B. Poulton, 'Colours of Animals,' 1890, pp. 142—146.

and turn brown, and after this change the dark colour is highly protective. It is also of especial importance for the cocoon to be well concealed during the winter months, when insect-eating animals are pressed for food, and are obliged to search for it with extreme care." An experiment with *Halias prasinana* is then described, in which a larva which had begun to spin a *brown* cocoon on an oak-leaf was transferred to a white box, where it subsequently spun a *white* cocoon.

If it were really established that there is an intimate relation of this kind between the colour of the cocoon and that of the substances to which it is attached, the fact would be very surprising, and perhaps unparalleled. We have here to deal with a case not of a graduated resemblance between the general tint of the skin of an animal and that of the ground on which it lies, such as is found in many forms which are provided with contractile or moveable chromatophores (the Sole, *Sepia*, &c.), but of a resemblance between the colour of external objects and that of a secreted substance poured out upon them. The existence of such a phenomenon, if proved, would introduce new possibilities into physiology.

It is, of course, believed that this power of adapting the colour of the cocoon is a protection from enemies, and it is suggested that as such it may have arisen and been perpetuated by Natural Selection. To this view there is an objection which may be widely applied in like cases, but which in this one has particular force. The belief that the resemblance between the cocoon and adjacent objects protects the insect is based on expectation and not on evidence. If we ask from *what* enemies the insect is thus protected, we are told from insectivorous enemies; and here the matter must rest. There is as yet no direct evidence that a definite bird or mammal, for instance, has ever been seen to open a cocoon of *S. carpini* or *E. lanestris;* still less that any such animal habitually searches for these cocoons. In the case of *S. carpini*, at least, it may be plausibly argued that, so far as *a priori* impression goes, it is unlikely that these cocoons are sought by birds, for the wall of the cocoon is so tough that it must be difficult for most birds to pierce it. No doubt rats and mice could gnaw through them, but it is likely that these animals, which are for the most part nocturnal, depend for their supply

of food at least as much on the sense of smell as on that of sight.

It may be remarked in passing that there is abundant evidence that the larvæ of these insects are infested by *Tachina*, and by hymenopterous parasites, and, as in other cases, probably these are really their most formidable enemies.

As to their enemies in the pupal state, there is no evidence. In the absence of such evidence it may be contended that any disquisition on the modes by which they may be protected from hypothetical enemies is premature. This, however, is a line of argument of which Mr. Poulton and the apologists of Adaptation are well aware, and to which they expose themselves avowedly.

The fact, however, that the colour of these cocoons varies in accordance with that of adjacent substances did not seem, in my judgment, to be established beyond possibility of question, and it was in the belief that some simple sources of error were not excluded that the following experiments were undertaken.

Eriogaster lanestris.—I. A large colony of these caterpillars were brought home, they being then about three-quarters grown, and fed in a large plain glass vessel till Aug. 15th. On that date the whole was examined, and 11 cocoons were found spun on leaves. Of these 6 were of full colour—

4 were dark, but not quite so full in colour.
1 was a good deal lighter, but still brown.

The dark colour is about the tint of black coffee, and the lighter specimen may be described as having the colour of strong tea with some milk it. It will be convenient to refer to this specimen for comparison, and its tint may be spoken of as "half-colour."

II. From this colony a number were chosen which seemed to be ready to spin These were shut up in a white muslin bag full of torn, crumpled strips of white paper. Of these larvæ several died, but five survived, and all spun cocoons attached to the muslin, or to the white paper, or to both. Of these five—

3 were quite white.
2 were very pale cream-colour.

The paper and bag were bespattered with a brown juicy substance, which will be described later.

III. A number of apparently full-fed larvæ were similarly chosen and shut up in *dark* substances, and of these six survived and spun as follows :—

a. In black gauze, 1 specimen. Cocoon lighter than "half-colour."

b. On brown paper in green muslin bag, 2 specimens. Both quite white.

c. On brown dried leaves in a green muslin bag, 2 specimens. One white; one very pale cream-colour.

d. In the same bag of leaves as *c*; spun on the green muslin, 1 specimen. Cocoon white.

All these six cocoons, attached to dark substances, were of light colour. There was a good deal of brown evacuation, as in II.

IV. Two larvæ, which had begun to spin in leaves, were taken out and shut up in white paper. Both spun cocoons of light colour.

One larva, which had similarly begun to spin in a leaf, was taken out, and it eventually spun a white cocoon between green gauze and a piece of clear glass.

One larva, beginning to spin on white paper, was disturbed, and afterwards spun a white cocoon.

Therefore, of 4 larvæ which were disturbed while spinning, all spun light cocoons, 1 being on a dark substance, 3 being on white substances.

These results leave little room for doubt that the absence of colour in the cocoons results from an unnatural condition, such as disturbance at the time of spinning, or removal from food-plant when the growth is nearly complete. Besides these the presence of parasites should be mentioned as sometimes associated with a similar effect. This was seen once in a specimen of *E. lanestris*, and once in *S. carpini*, which were inhabited by a *Tachina*. In both these cases the cocoons were quite white. On the other hand, several *Tachinæ* were found in one *Saturnia* cocoon of *dark* colour. It will be seen, therefore, that though these observations fully confirm the statement that the larvæ do spin dark cocoons on the leaves, and white cocoons when confined in white paper, yet they suggest that the operating cause is the confinement and not the whiteness of the

paper. The nature of the distinction between brown and white cocoons is discussed below.

V. From these experiments it appeared that light-coloured cocoons were produced when the larvæ were confined in white substances, and also when they were confined in dark substances, but that when left with their food the cocoons were dark. This result suggested that perhaps the alteration of colour was brought about by some unhealthy condition associated with the removal of the larvæ from their food. The four larvæ which had been disturbed whilst spinning also produced white cocoons, though one of them was attached to a dark object. From this it seemed likely that disturbance at the time of spinning might also be sufficient to prevent the cocoon from being properly coloured. It became therefore necessary to see what coloured cocoons would be spun by larvæ which of their own free will spun upon white paper. With this object the vessel in which the remaining larvæ were feeding was carefully filled with crumpled white paper, so that each twig of food (hawthorn) was more or less surrounded with paper. All the larvæ in this vessel chose to spin in the paper, and 15 cocoons were thus obtained. Of these 15 cocoons on white paper—

4 were of full colour.
6 were lighter than this, but still substantially brown.
4 were light, 3 of them being white.

Of the 3 which were white, one was spun by one of four larvæ which remained at the last, and were not fed owing to a mistake.

To recapitulate:—Of 11 larvæ left with their food, all spun dark cocoons on leaves.

Of 14 larvæ left with their food and white paper, 10 spun dark cocoons on white paper, and 4 spun light cocoons on white paper.

Of 11 larvæ which were shut up, all spun light cocoons, 5 being on white substances, and 6 being on dark substances.

Saturnia carpini.—Eleven cocoons found spun in the hedges in a state of nature were all of full colour.

Experiments made with larvæ of this species agreed generally with the results from those made on *E. lanestris*,

but I found it difficult to obtain any considerable number of dark cocoons from *carpini* larvæ in captivity, even when they were left with their food, and disturbed as little as possible.

Fifteen larvæ, which were shut up in various dark substances, such as brown paper, black muslin, green muslin, &c., spun cocoons which were all light in colour, though attached to dark substances, several being quite white. No dark cocoon was spun by any larva thus confined.

Fifteen larvæ were fed in a large vessel on food surrounded with crumpled white paper, treated as the *Eriogaster* larvæ were in experiment V. Of these 15, only 7 spun dark cocoons; but of these, 3 were more or less attached to white paper, the remaining 4 being among leaves.

4 were light brown in colour, being attached to both twigs and paper.
4 were white or nearly so, being attached to paper and leaves.

From this it seems to be difficult to get conditions which are sufficiently healthy to enable the larvæ to spin dark cocoons, but it does not appear that the colour of the cocoons depends upon that of foreign substances.

Most of the bags and vessels in which the larvæ were confined were found to be bespattered with brown fluid similar to that which was seen in the case of the *Eriogaster*.

The colouring substance of the cocoons.—It has been mentioned that many of the larvæ of *Eriogaster* and of *Saturnia* evacuated a quantity of brown fluid substance. The tint of this fluid so closely matches that of the brown cocoons that it seems possible that their colour may be given to them by an outpouring of the brown fluid upon them. In view of this possibility the nature of this fluid is a matter of interest, and the following facts relating to it have a bearing on the question of the coloration of cocoons.

The brown fluid was found only in vessels in which large and presumably full-fed larvæ were living. In cases in which a larva was removed and shut up, it was generally present on the second or third day after removal, but there were several large patches of it in the

large vessel in which the *Saturnia* larvæ were kept without disturbance. The fluid itself is viscous, and of a dark coffee-brown colour, closely resembling that of the cocoons. It generally contained some fœcal matter and particles of semi-digested food. From this, therefore, it may be concluded that the fluid is voided from the intestines, but I never saw a larva in the act of evacuating it. If this should be found to be the origin of the fluid, it may probably be looked on as being of the nature of "meconium."

The presumption that it is with this fluid that the cocoons are coloured rests on the following observations: A considerable number of larvæ, which were known to have voided the brown fluid, spun white cocoons. On the other hand, many spun white cocoons which were not known to have voided any fluid, though nevertheless they may have done so. Next, it was observed that some of the dark *Saturnia* cocoons, after they were just finished, were wet, as though drenched with brown fluid. Several also of the pale *Saturnia* cocoons had a darker patch in one part, generally upon the neck of the cocoon, though in one case there was a dark patch on the side. The appearance of these patches was exactly as if a quantity of brown fluid had been ejected upon the inside of the cocoon. In one case a brown cocoon of *Saturnia*, which was spun against a piece of white paper, lay on a large stain of the brown fluid; and there could be little doubt that the fluid had soaked through the cocoon on to the paper.

There is, then, good evidence that a brown meconial fluid is voided by caterpillars which are removed and shut up before they spin, and if it were to be established that the colouring matter of the cocoons is due, or largely due, to this fluid, the phenomenon of the colour-variation of cocoons becomes much simpler; for the cocoons of secluded larvæ are, on this hypothesis, white by reason of the previous voiding of the brown fluid, and the consequent absence of a supply of colouring matter.

It should be mentioned, as making against this view, that in the case of three *Eriogaster* larvæ, which were disturbed whilst spinning, and which afterwards spun white cocoons, it was almost certain that no brown fluid was previously voided. It is, of course, possible that the

shock of disturbance may have led to a retention of the brown fluid, though this cannot be proved.

After these experiments were performed I received information that Mr. Poulton* and Prof. Meldola have shown that the cocoon of *Eriogaster* is largely made up of oxalate of lime, which is deposited on the first thin web of silk. There was no direct evidence as to the manner in which this substance is deposited, but it was believed to be voided from the intestine. This observation would thus to some extent give support to the suggestion here made, that the colouring matter of the cocoons is produced chiefly, if not altogether, from the intestine.

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* In a paper read before the Physiological Society, not yet published (February, 1892).